Late Pleistocene Megafaunal Deposits on the Isthmus of Panama and Their Paleoenvironmental Implications

GEORGES A. PEARSON

Department of Anthropology, University of Kansas, 622 Fraser Hall, 1415 Jayhawk Blvd., Lawrence, KS 66045-7556, USA ftgap@ku.edu

ABSTRACT.—Two megafaunal deposits were discovered next to the villages of La Trinidaíta and Llano Hato during an archaeological survey on the Azuero Peninsula of Panama. The fossil sites were found near other localities first reported in 1957 by Smithsonian paleontologist Lewis Gazin. Bones at La Trinidaíta and Llano Hato rested in tight horizontal clusters at the bottom of ancient creeks and ponds. The remains appear to have been buried rapidly by thick deposits of fine clay when environmental conditions were wetter and cooler than today. Animals identified at La Trinidaíta and Llano Hato include Cuvieronius tropicus, Eremotherium sp., and some turtles. Radiocarbon-dated charcoal fragments associated with the bones gave contemporaneous dates of $44,840 \pm 700$ and $47,040 \pm 900$ ¹⁴C yr B.P. These dates indicate that carcasses accumulated during the Marine Isotope Stage 3 (MIS3) interstadial. Because other fossils were not found above or below these principal deposits, it is argued that the MIS3 environment was especially favorable for supporting large browsers and mixed-feeders and preserving their bones on the landscape. These environmental and taphonomical characteristics likely disappeared as the climate of the lowland Neotropics became drier in response to the following arid glacial advance. During this time, C4 plants dominated the landscape and may have forced gomphotheres and giant ground sloths to abandon the dry Pacific lowlands and follow the rising tree-lines. Such large-scale range re-organization may have caused animals to abandon some regions of lower Central America during the Last Glacial Maximum.

KEYWORDS.—Panama, megafauna, MIS3, Cuvieronius, Eremotherium, Rancholabrean, Pleistocene.

INTRODUCTION

During the late Pliocene and the Pleistocene, Central America acted as a connecting corridor that allowed North and South American animal species to intermingle. This process, called the Great American Faunal Interchange (Marshall et al. 1982; Stehli and Webb 1985; Marshall 1988; Webb 1991, 1997), began approximately 3 MYA with the final emergence of the Panamanian land bridge and closure of the last marine corridor between the Pacific and Atlantic oceans (Coates 1997). Among the northern animals that crossed the Isthmus into South America were gomphotheriids (Cuvieronius), horses, llamas, deer, peccaries, tapirs, and rabbits (Webb 1991). Immigrants from the south included several

types of armadillos (Holmesina, Glyptotherium, Chlamydotherium), ground sloths (Megalonyx, Eremotherium, Glossotherium), toxodonts (*Mixotoxodon*), porcupines, opossums, anteaters, and monkeys. Initially, the dispersal of animals across the Isthmus was facilitated by the presence of a continuous savanna corridor spanning both continents (Webb 1978, 1991). By the end of the Pleistocene, however, a more humid environment began to prevail in lower Central America, which culminated in the modern Neotropics. With time, the increasingly hot and wet expanse between Nicaragua and Panama became less of a conduit and more of a filter, gradually preventing animal and plants from traversing to and from the continents. Although the emergence of the Isthmus of Panama was responsible for the terrestrial swapping of animals, very few fossils have been recovered on the land bridge itself. The first discoveries were reported by Gazin in 1957 who excavated two

ms. received August 16, 2004; accepted December 21, 2004

megafaunal localities on the Azuero Peninsula. The first site, La Coca, near the town of Ocú, contained the remains of *Eremotherium* and *Mixotoxodon* (originally described as *Toxodon*, Gazin 1957:346). At the second locality, El Hatillo, Gazin (1957:347) identified the bones of *Eremotherium*, *Equus*, *Cuvieronius*, *Glyptodon*, *Pseudemys* (*Trachemys*), and *Glossotherium* among others. Here I report the discovery of two additional fossil deposits found near Gazin's original sites.

METHODS

In 2001, I conducted an archaeological survey whose main objective was to locate late Pleistocene-early Holocene human occupations on the Azuero Peninsula (Pearson 2002; Pearson and Cooke 2002). Because Paleoindian sites sometimes contain the remains of megamammals (Grayson and Meltzer 2002), ancient bone deposits were also sought to determine if a human presence might be associated with some of them. During the reconnaissance, bones of extinct megafauna were discovered next to the small villages of Llano Hato and La Trinidaíta.

Both the Llano Hato and La Trinidaíta localities were excavated following archaeological protocols. Using a theodolite, horizontal grids of 1 m² excavation units were established over the extent of the work area. These grids were oriented along magnetic north or an arbitrary site north. Excavations proceeded by shovels and trowels to remove sterile overburden followed by wooden shish kebab sticks to expose the bone beds. Because fossils were embedded in a moist and sticky clay matrix, sieves were not used in the field. Most bones were in a very poor state of preservation and had to be treated in the field with a solution of diluted white glue and in the laboratory with an acetone-based consolidant (Acryloid B-72). The absence of human-made artifacts coupled with a suite of early radiocarbon dates later confirmed that the deposits represented non-cultural paleontological accumulations. Following the excavations, bone elements with visible identifying features were shipped to the

Florida Museum of Natural History in Gainesville where the author conducted preliminary identification. Fossils were eventually returned to the Smithsonian Tropical Research Institute in Panama where they are presently stored.

RESULTS

La Trinidaíta

Setting.—La Trinidaíta (98 m a.s.l.) is located approximately 9 km west of the town of Pesé (UTM: 17NNU533942873738, NAD 27) (Figure 1). The site was discovered in a small topographic depression that drains into a small creek and becomes boggy during the rainy season (Figure 2). The bowl is delineated by a gentle northern slope and eroding sidewalls to the south. Although the land was in a fallow state at the time of our study, it had previously served to grow tubers. Prior planting and harvesting activities had exposed bones along the shallow edges of the depression.

Excavations at La Trinidaíta were oriented perpendicular to the draining axis of the basin in order to sample a cross-section of the sloping deposits. A 2 m² test pit (TP1) was placed near the bottom of the bowl aligned with a narrow trench (TR1) and a second test pit (TP2, 1 m²) along its slope. In addition, several test pits were dug at a distance from the main excavation area to determine the extent of the fossil-bearing deposit. All bones recovered during the study were found in TP1, TP2, TR1, and unit N80E122.

Stratigraphy and dating.—Bones at La Trinidaíta were first observed on the surface of the northern incline. These fossils were protruding from a 10 cm-thick plowzone observed in the stratigraphic profile of the trench. Specimens recovered *in situ* in TR1 were resting on an ancient creek bed composed of rounded cobbles and sand lying immediately above the bedrock (Figure 3). Fossils were encased and overlaid by fine clay which thickened progressively towards the bottom of the basin (from 25 cm in TR1 to over a meter in TP1). Although our excavations did not reach the rocky substrate in TP1, megafaunal remains were

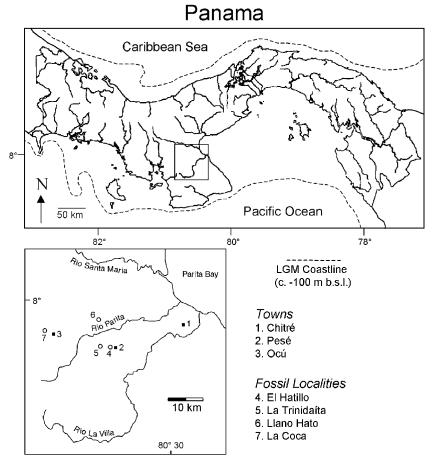


FIG. 1. Map of Panama and Azuero Peninsula (above) and inset map (below) showing towns (solid squares) and fossil localities (open circles) described in text.

found at 85 cm below surface within the fine clay deposit (Figure 4). A charcoal sample collected approximately 15 cm below an isolated *Eremotherium* vertebra in TP1 gave a date of $44,840 \pm 700^{-14}$ C yr B.P. (Beta-158916, Table 1). This date is considered an average age because the charcoal sample was recovered under some of the fossils in clay that buried the main bone bed. Several remains were also collected from TP2 but excavations in this test unit were incomplete due to in-filling of water during heavy rains. The bone-rich clay was not observed in units N100E128 and N115E88-89.

Fossil remains.—At least three genera were identified at La Trinidaíta (Table 2, Figure 5). The majority of bone elements

consisted of Eremotherium vertebrae. Depending on the taxonomic scheme one wishes to adopt, late Pleistocene ground sloth species from Panama belong to either E. laurillardi (Cartelle and De Iuliis 1995) or to E. rusconi (Guérin and Faure 2000). Cuvieronius tropicus was represented by a tooth fragment (Figure 6), a complete tibia, some vertebrae, and a proximal rib. Finally, a small section of carapace was ascribed to an unidentified terrestrial turtle. Regrettably, it was not possible to classify many fragmentary specimens (n < 80) and the MNI count for this collection must tentatively remain at one individual for each species.

Bones did not show obvious signs of surface weathering such as root etching, insect

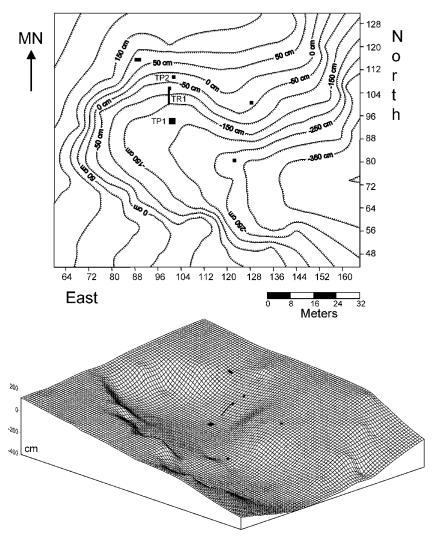


FIG. 2. Topographic map of the La Trinidaíta fossil locality, Panama. Test pits and trenches are indicated by solid squares and rectangles respectively.

burrows, rodent gnawing, or desiccation cracks and exfoliation. This evidence suggests that the animals died at the watering hole and carcasses were deposited in the aqueous environment of the creek. Many of the bones were stained by ferrous oxide giving them a brick-colored hue. The fossils were trapped in a humid matrix and had to be treated in the field and allowed to dry gradually before they could be removed.

Llano Hato

Setting.—The Llano Hato site (105 m a.s.l.) is situated approximately 14 km northwest of

Pesé (UTM: 17NNU533587881887, NAD 27). The site was discovered in a cow pasture on the edge of a small, seasonal stream (Quebrada El Jobo). A 2 m² test pit (TP1) was excavated near the eastern bank where bones were eroding out of the downcut channel (Figure 7). Five shovel tests (50 cm²) were also dug along the creek in an effort to follow the fossil-bearing clay encountered in TP1. Megafaunal bones were not, however, discovered in these shallower test units.

Stratigraphy and dating.—TP1 was excavated to a depth of two meters. With the

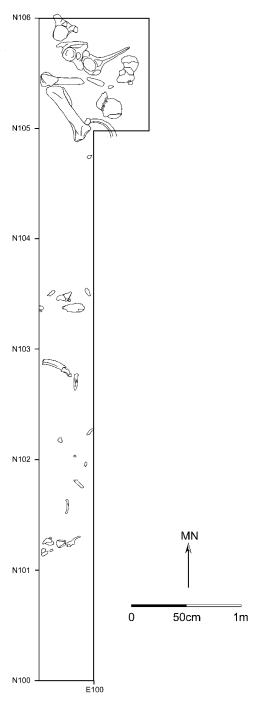


FIG. 3. La Trinidaíta fossil locality, test trench No.1.

exception of some discontinuous tephra lenses, the deposits seen in the stratigraphic profile were composed entirely of fine clay (Figure 8). This clay was present in all shovel tests along the eastern edge of El Jobo Creek. However, clay was not observed in our test unit on the other side of the furrow. Sediments on the western bank were shallow and extremely rocky.

Three AMS radiocarbon dates were secured from TP1 (Table 1). The first came from a collagen sample extracted from an untreated Eremotherium rib head. It provided a date of 2770 \pm 90 ¹⁴C yr B.P. (CAMS-77491) (Figure 9). This improbable age may have been caused by a major alteration of the specimen's geochemistry (T. Stafford, pers. comm. 2001). A second date of $47,040 \pm 900^{-14}$ C yr B.P. (CAMS-78192) was obtained from a piece of charcoal found within the bone bed. Lastly, a piece of hardened clay and tephra containing charcoal fragments, collected approximately 50 cm above the fossils, was dated at $21,490 \pm 120^{-14}$ C yr B.P. (Beta-158915).

Fossil remains.—Bones recovered from TP1 were in a very poor state of preservation compared to specimens from La Trinidaíta. Although fossils did not show evidence of damage produced by prolonged exposure in open environments, the majority exhibited mosaic patterns of cracks and flaking (Behrensmeyer 1978:153). This type of weathering may result from repeated cycles of bone swelling and shrinking caused by a seasonally-fluctuating water table. In this manner, fossils appear to mimic the physical responses of the clay in which they were deposited. Although bones were treated in the field with diluted white glue, many crumbled upon drying.

Animals represented at Llano Hato included *Eremotherium* sp. and at least one genus of turtle (Table 3, Figure 5). Many of the identifiable sloth elements were small and unfused, suggesting that at least one juvenile was present. However, because the bones were so badly preserved, it was impossible to determine if all the remains belonged to one or more individual sloths.

DISCUSSION

The bone assemblages from La Trinidaíta and Llano Hato appear to have accumulated between c. 47,000 and 45,000 14 C years

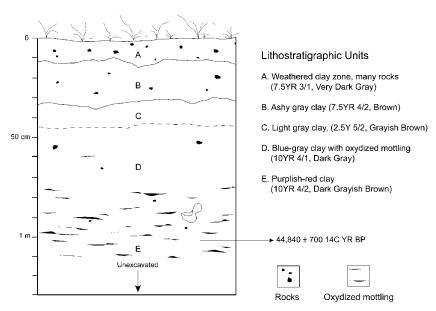


FIG. 4. Stratigraphic profile of La Trinidaíta deposits (north wall, TP1).

TABLE 1. Radiocarbon dates from Panamanian magafaunal localities.

Site	Cat. no.	¹⁴ C yr BP	Material	¹³ C/ ¹² C	Method
Llano Hato	Beta-158915	21,490 ± 120	soil organics	-23.1%	AMS
Llano Hato	CAMS-78192	$47,040 \pm 900$	charcoal	not given	AMS
Llano Hato	CAMS-77491	2770 ± 90	bone collagen	not given	AMS
La Trinidaíta	Beta-158916	$44,840 \pm 700$	charcoal	-27.3%	AMS

ago during the interstadial of Marine Isotope Stage 3 (MIS3, c. 60,000-30,000 years BP). The remains were found clustered horizontally, indicating relatively rapid accretion and burial. Significantly, no other fossil concentrations appear to have formed before or after the main beds described in this report. The geomorphological contexts of both localities were similar, supporting the idea that the bone accumulations are of the same time period and formed under comparable paleoenvironmental conditions. Both assemblages were found buried in fine clay matrices that were apparently built up by low-energy water systems. A third fossil site not described here—Cerro Gordo near Llano Hato-was also located in a similar geomorphological context. This site was found in a clay-filled depression where a farmer discovered a Cuvieronius t. molar. As for the stratigraphic contexts of the 1950s discoveries, Gazin's descriptions of the El Hatillo and La Coca sites recall both La Trinidaíta and Llano Hato respectively:

[at El Hatillo] The bones were found to occur at the bottom of the mud near contact with the underlying bedrock, close to the surface at the periphery but increasing in depth towards the spring. (Gazin 1957:343)

At La Coca the remains were preserved on the upper surface of a low terrace (pl. 3). The materials were here found weathering out of the thin superficial remnant of mud and gravel, and the spring associated with the occurrence and possibly related to the entrapment is now flowing out from the steeper slopes below the terrace top. This suggests that the shallow ravine below the terrace had been cut since the fossil accumulation was formed. (Gazin 1957:348)

Table 2.	List of	fossil	remains	from	La	Trinidaíta
locality, Az	uero Pe	eninsul	a, Panan	ıa.		

Cat. no.	Element	Genus, species
LT00	Right clavicle	Eremotherium sp
LT01a	Vertebra fragment	Eremotherium sp.
LT01b	Caudal vertebra, chevron bone	Eremotherium sp
LT16	Vertebra fragment	Eremotherium sp.
LT29	Vertebra fragment (axis?)	Eremotherium sp.
LT30	Caudal vertebra	Eremotherium sp.
LT36	Vertebra fragment	Eremotherium sp.
LT39	Tooth fragment	Eremotherium sp.
LT51	Tooth fragment	Cuvieronius t.
LT55	Vertebra fragment	Eremotherium sp.
LT62	Caudal vertebra	Eremotherium sp.
LT64	Caudal vertebra	Eremotherium sp.
LT75	Right pes bone	Eremotherium sp.
LT85	Turtle carapace fragment	Trachemys sp.?
LT87	Rib fragment	Cuvieronius t.
LT92	Rib fragment	Eremotherium sp.
LT93	Left fibula	Cuvieronius t.
LT94	Left distal femur	Cuvieronius t.
LT95	Right distal fibula	Cuvieronius t.
LT96	Sternal bone	Cuvieronius t.
LT97	Sesamoid	Eremotherium sp.
LT100	Left tibia	Cuvieronius t.
LT101	Thoracic vertebra	Cuvieronius t.
LT102	Thoracic vertebra	Cuvieronius t.
LT103	Thoracic vertebra	Cuvieronius t.

Taking all of these sites into consideration, one might ask if these megafaunal deposits might not represent a time when bone accumulation and/or preservation were taphonomically favorable on the Azuero Peninsula. To answer this questions we must first try and reconstruct the environment that prevailed on the Isthmus during this time.

If we examine the modern environmental conditions on the Azuero Peninsula, it becomes quite obvious that the hydrographic systems during MIS3 were radically different. Then, as is now, the Isthmus received most of its annual precipitation when the Intercontinental Convergence Zone (ITCZ) moved above the Equator between the months of May and November. Today, the annual rainfall (c. 1500-2500 mm) and evapotranspiration rates in north central Azuero cannot maintain natural standing bodies of water during the dry season and most creeks disappear. Cattle introduced

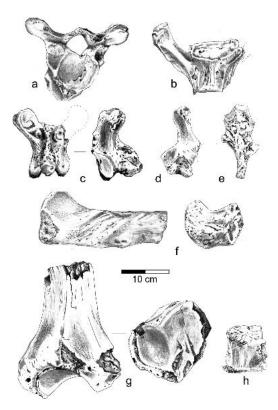


FIG. 5. Fossil remains from La Trinidaíta and Llano Hato sites: a) thoracic vertebra *Cuvieronius t.* (#LT-101); b, c, d) caudal vertebrae *Eremotherium* sp. (#LT-62, 30, 64); e) sternal bone *Cuvieronius t.* (#LT-96); f) right clavicle *Eremotherium* sp. (#LT-00); g) right distal tibia *Eremotherium* sp. (#LH-00); h) vertebra *Eremotherium* sp. (#LH-16), (see Tables 2 and 3).

on the peninsula face yearly starvation and dehydration if owners do not supplement their diet and dig wells or artificial catchments to provide them with fresh water. Current levels of deforestation resulting from modern ranching and subsequent soil denudation have exacerbated this situation.

In view that there are now very few perennial water sources anywhere on the Azuero and the accumulation of thick clay deposits is no longer a common geological process, can we speak of a higher annual rainfall in Panama during MIS3? Data from the Greenland Ice Sheet Project 2 (GISP2) (Grootes et al. 1993; Dansgaard et al. 1993) indicate that MIS3 was itself marked by frequent short, wetter interstadials (Dansgaard/Oeschger or D/O events) interspaced by dry, cooler periods (Heinrich

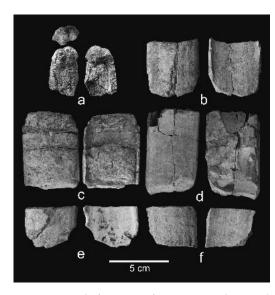


FIG. 6. Tooth fragments from La Trinidaíta and Llano Hato showing exterior enamel (first view) and interior dentine (second view): a) molar fragment of *Cuvieronius t.* (#LT-51); b-f) *Eremotherium* sp. (#LH-64, #LT-39, #LH-01, #LH-45, #LH-19), (see Tables 2 and 3).

events). Although the global mechanisms for these climatic changes are still being investigated, the saw-tooth profile of the GISP2 δ¹⁸O values clearly demonstrate that the transitions between D/O and Heinrich events were sometimes quite rapid (in some cases only 25 years according to Burns et al. [2003]) and of considerable magnitude. Information gathered from marine cores drilled in the Cariaco Basin (Peterson et al. 2000) and off the island of Grenada (Vink et al. 2001) have shown that deposition of organic carbon and terrigenous sediments, originating from northern South America, was relatively high during the D/O interstadials due to high rainfall and river discharge. Moreover, Peterson et al. (2000:1950) suggest that "higher interstadial rainfall along the coastline of South America may have led to a higher net export of moisture to the Pacific" across the Isthmus of Panama. Increased monsoonal activity during D/O events has also been observed in terrestrial and marine proxy records from Asia (Wang et al. 2001; Stott et al. 2002; Yuan et al. 2004) and the Arabian Sea (Schulz et al. 1998; Leuschner and Sirocko 2000). Thus, these data indicate that the ITCZ hovered long enough above the Isthmus during D/O interstadials to provide the land bridge with equal or higher annual precipitation than today. These conditions may have also shortened the dry seasons and lead to more humid and verdant landscapes on the Pacific side of Panama.

Describing the vegetation cover that prevailed on the Azuero during this time is more difficult due to a scarcity of Pleistocene-age pollen cores. Only a few palynological and phytolith studies in lower Central America and northern South America (Van der Hammen 1974; Bush and Colinvaux 1990; Hooghiemstra et al. 1992; Behling et al. 1998) have allowed us to reconstruct the plant communities that existed before the Last Glacial Maximum (LGM). These studies have revealed that the MIS3 climate in this part of the Americas was cooler and perhaps even wetter than during the Holocene. Forests were depressed by thousands of meters in some zones and grassland/savannas were probably limited to a few coastal fringes. The co-occurrence of both Eremotherium and Cuvieronius in the same deposits supports the idea that these animals lived in open forest environments and that gomphotheres were probably mixed C_3 - C_4 feeders (Sánchez et al. 2004). It is thus safe to conclude that lower evapotranspiration during the dry season coupled with equal or slightly higher annual precipitation on the Isthmus were probably sufficient to maintain flowing creeks and shallow ponds during most of the year. If the Azuero Peninsula was indeed strewn with watering holes before the LGM, then these areas would have acted as natural bone traps. Thus, the geomorphological characteristics that prevailed during the interstadial would explain the high paleontological visibility of MIS3 megafaunal remains on the Azuero.

Following the MIS3 interstadial, the climate became extremely arid as lowered surface sea temperatures depressed the ITCZ further south (Peterson et al. 2000). During this time, annual rainfall dropped 35-50% across Central America and northern South America (Leyden 1985; Piperno

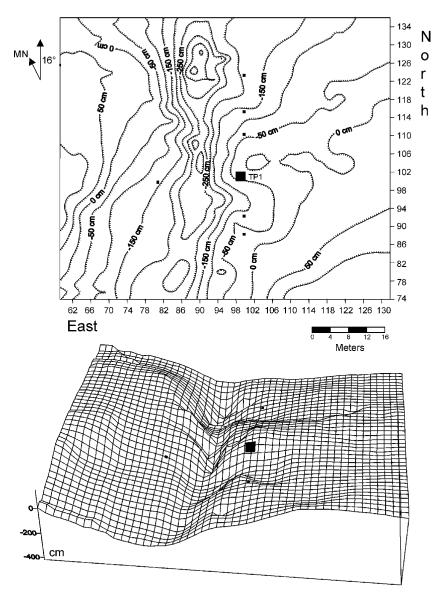


FIG. 7. Topographic map of the Llano Hato fossil locality, Panama. Test pits and trenches are indicated by solid squares and rectangles, respectively.

and Jones 2003). The Pacific lowland of Panama, for example, became a savanna-like expanse after mixed C_3 - C_4 ecosystems were replaced by C_4 dominated plant communities during the last glacial (Piperno and Jones 2003:85). This major reorganization of the vegetation may have forced some browsers and mixed-feeders in parts of Central America to shift their ranges towards wetter areas. Increasing aridity

could have forced gomphotheres and sloths to abandon the Pacific lowlands of Panama and follow the rising tree-lines along the Continental Divide or the southwestern highlands on the Azuero. Another possibility is that these animals began to concentrate along larger river systems that flowed throughout the year. Xeric conditions may have also accelerated surface erosion and prevented megafaunal remains

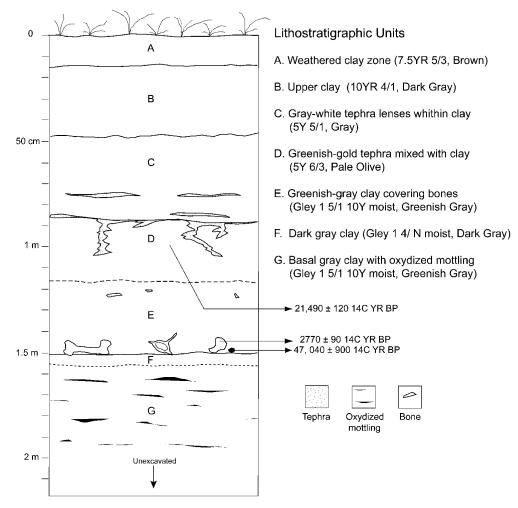


FIG. 8. Stratigraphic profile of Llano Hato deposits (west wall, TP1).

from being buried in more open landscapes. Therefore, the apparent absence post-LGM fossils in this part of the Azuero could be a reflection of unfavorable taphonomic conditions during this dry period. Sampling strategies for future paleontological research on the Azuero should concentrate on river terraces, caves, and natural springs as these may be the only areas where late megafaunal remains were preserved.

CONCLUSION

The Great American Faunal Interchange between North and South America began

approximately 3 MYA with the final closure of the Panamanian land bridge. Although the Isthmus of Panama was responsible for this large scale intermingling of biota, very few fossils have actually been found here. For over forty years, the only available descriptions of Panamanian megafauna were those provided by Gazin (1957) from the La Coca and El Hatillo sites. Recent work at La Trinidaíta and Llano Hato has not only identified additional sources of fossils on the Azuero, but also provided secure radiocarbon dates for extinct megafauna in lower Central America. Charcoal associated with the remains gave contemporaneous dates of $44,840 \pm 700$ and

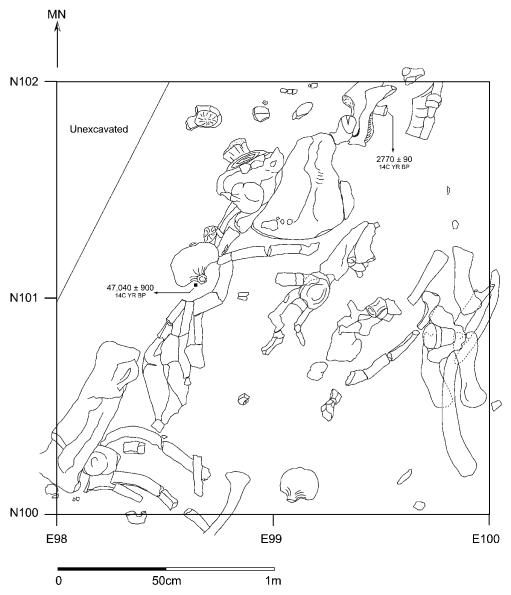


FIG. 9. Bone bed and radiocarbon dates, TP1, Llano Hato, Panama.

 $47,040 \pm 900^{-14}$ C yr B.P. indicating that the bone beds formed during the MIS3 interstadial. Significantly, fossils were discovered buried under thick fine clay deposits at the bottoms of paleo-creek beds and ponds. The geomorphological contexts at these localities suggest that bones accumulated at a time when the Azuero Peninsula was cooler and wetter than today. Gradual replacement of mixed C_3 - C_4 plant communities by C_4 dominated ecosystems, during

the LGM, may have shifted some megafaunal feeding ranges on the Pacific watershed lowlands of Panama. Thus, the Pleistocene biogeographic distributions on this narrow land bridge were likely quite dynamic due to its role as a passageway between the continents and the frequency of stadial-interstadial climatic oscillations.

Acknowledgments.—I am eternally grateful to my good friend Robert A. Beckwith

TABLE 3. List of fossil remains from Llano Hato locality, Azuero Peninsula, Panama.

Cat. no.	Element	Genus, species
LH00	Right distal tibia	Eremotherium sp.
LH01	Tooth fragment	Eremotherium sp.
LH04	Rib fragment?	Eremotherium sp.
LH05	Rib fragment	Eremotherium sp.
LH06	Proximal humerus	Eremotherium sp.
LH13	Cranial fragment?	Eremotherium sp.
LH16	Vertebra	Eremotherium sp.
LH17	Vertebra fragment	Eremotherium sp.
LH18	Vertebra	Eremotherium sp.
LH19	Tooth fragment	Eremotherium sp.
LH21	Vertebra fragment	Eremotherium sp.
LH22	Tooth fragment	Eremotherium sp.
LH24	Vertebra fragment	Eremotherium sp.
LH26	Vertebra fragment	Eremotherium sp.
LH29	Vertebra	Eremotherium sp.
LH31	Sternum	Eremotherium sp.
LH32	Rib	Eremotherium sp.
LH34	Turtle carapace	Trachemys sp.?
1 1 107	fragment?	E 4 :
LH37	Rib fragment	Eremotherium sp.
LH39	Turtle plastron fragment?	Trachemys sp.?
LH43	Right femur	Eremotherium sp.
LH44	Rib fragment	Eremotherium sp.
LH45	Tooth fragment	Eremotherium sp.
LH49	Right clavicle	Eremotherium sp.
LH51	First rib fragment	Eremotherium sp.
LH54	Rib	Eremotherium sp.
LH55	Carpal (?)	Eremotherium sp.
LH56	Rib	Eremotherium sp.
LH57	Unfused articular	Eremotherium sp.
	surface of centrum	
LH58	Rib head	Eremotherium sp.
LH59	Rib head	Eremotherium sp.
LH60	Turtle caparace	Trachemys sp.?
LH64	Tooth fragment	Eremotherium sp.
LHxx	Claw fragment	Eremotherium sp.

who assisted me throughout this project. A special thanks goes to Panamanian land owners and local workers who lent a hand during the excavations: Cesar A. Serrano C., E. Alfonso Tejada Caballero, Luís Carlos Vasquez Barba, Jesús Nieto Alvarado, Alberto E. Ruíz de León, and Erasmo Fung. Funding for this research was provided by a Pre-Doctoral fellowship from the Smithsonian Tropical Research Institute (STRI). This investigation could not have been carried out without the support of Richard Cooke and Dolores Piperno of the STRI.

Carlos Fitzgerald of Patrimonio Histórico was instrumental in alleviating some of the logistical headaches of fieldwork. Alberto E. Ruíz de Leon provided the fossil drawings. Finally, I would like to extend a special debt of gratitude to S. David Webb of the Florida Museum of Natural History, as well as C. Andrew Hemmings, and Gary S. Morgan who made my stay in Gainesville all the more productive.

LITERATURE CITED

Behling, H., A. J. Negret, and H. Hooghiemstra. 1998. Late Quaternary vegetational and climatic change in the Popayán region, southern Colombian Andes. *Journal of Quaternary Science* 13:43-53.

Behrensmeyer, A. K. 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4: 150-162

Burns, S. J., D. Fleitmann, A. Matter, J. Kramers, and A. A. Al-Subbary. 2003. Indian Ocean climate and an absolute chronology over Dansgaard/Oeschger events 9 to 13. *Science* 301:1365-1367.

Bush, M. B., and P. Colinvaux. 1990. A pollen record of a complete glacial cycle from lowland Panama. *Journal of Vegetation Science* 1:105-118.

Cartelle, C., and G. De Iuliis. 1995. Eremotherium laurillardi: the Panamerican late Pleistocene megatheriid sloth. Journal of Vertebrate Paleontology 15(4): 830-841.

Coates, A. G. 1997. The forging of Central America. In Central America: A Natural and Cultural History, ed. A. G. Coates, 1-37. New Haven, Yale University Press.

Dansgaard, W., et al. 1993. Evidence for general instability of past climate from a 250-kyr ice-core record. *Nature* 364:218-220.

Gazin, C. L. 1957. Exploration for the remains of giant ground sloths in Panama. *Annual Report of the Board* of Regents of the Smithsonian Institution 1956. Publication No. 4272, 341-354. Smithsonian Institution, Washington.

Grayson, D. K., and D. J. Meltzer. 2002. Clovis hunting and large mammal extinction: A critical review of the evidence. *Journal of World Prehistory* 16:313-59

Grootes, P. M., M. Stuiver, J. W. C. White, S. Johnsen, and J. Jouzel. 1993. Comparison of oxygen isotope records from the GISP2 and GRIP Greenland ice cores. *Nature* 366:552-554.

Guérin, C., and M. Faure. 2000. La véritable nature de *Megatherium laurillardi* Lund, 1842 (Mammalia, Xenarthra): un nain parmi les geants. *Geobios* 33(4): 475-488.

Hooghiemstra, H., A. M. Cleff, G. W. Noldus, and M. Kappelle. 1992. Upper Quaternary vegetation dynamics and paleoclimatology of the La Chonta Bog area (Cordillera de Talamanca, Costa Rica). *Journal of Quaternary Science* 7:205-225.

- Leuschner, D. C., and F. Sirocko. 2000. The low-latitude monsoon climate during Dansgaard-Oeschger cycles and Heinrich events. Quaternary Science Review 19:243-254.
- Leyden B. W. 1985. Late Quaternary aridity and Holocene moisture fluctuations in the Lake Valencia Basin, Venezuela. *Ecology* 66:1275-1295.
- Marshall, L. G. 1988. Land mammals and the Great American Interchange. *American Scientist* 76:380-
- Marshall, L. G., D. S. Webb, J. J. Sepkoski, Jr., and D. M. Raup. 1982. Mammalian evolution and the Great American Interchange. *Science* 215:1351-1357.
- Pearson, G. A. 2002. Pan-continental Paleoindian expansions and interactions as viewed from the earliest lithic industries of lower Central America. Ph.D. University of Kansas.
- Pearson, G. A., and R. G. Cooke. 2002. The role of the Panamanian Land Bridge during the initial colonization of the Americas. *Antiquity* 76:931-932.
- Peterson L. C., G. H. Haug, K. A. Hughen, and U. Röhl. 2000. Rapid changes in the hydrologic cycle of the tropical Atlantic during the last glacial. Science 290:1947-1951.
- Piperno, D. R., and J. Jones. 2003. Paleoecological and archaeological implications of a late Pleistocene/ early Holocene record of vegetation and climate from the Pacific coastal plain of Panama. Quaternary Research 59:79-87
- Sánchez, B., J. L. Prado, and M. T. Alberdi. 2004. Feeding ecology, dispersal, and extinction of South American Pleistocene gomphotheres (Gomphotheriidae, Proboscidea). *Paleobiology* 30:146-161.

- Schulz, H., U. von Rad, and H. Erienkeuser. 1998. Correlation between Arabian Sea and Greenland climate oscillations of the past 110,000 years. *Nature* 393:54-58.
- Stehli, F. G., and S. D. Webb. 1985. *The Great American Biotic Interchange*. New York, Plenum Press.
- Stott, L., C. Poulsen, S. Lund, and R. Thunell. 2002. Super ENSO and global climate oscillations at millennial time scales. *Science* 297:222-226.
- Van Der Hammen, T. 1974. The Pleistocene changes of vegetation and climate in tropical South America. *Journal of Biogeography* 1:3-26.
- Vink, A., et al. 2001. Shifts in the position of the North Equatorial Current and rapid productivity changes in the western tropical Atlantic during the last glacial. *Paleoceanography* 16:1-12.
- Wang, Y. J., et al. 2001. A high-resolution absolutedated late Pleistocene monsoon record from Hulu cave, China. *Science* 294:2345-2348.
- Webb, D. S. 1978. A history of savanna vertebrates in the New World. Part II: South America and the Great Interchange. *Annual Review of Ecology and Systematics* 9:393-426.
- Webb, D. S. 1991. Ecogeography and the Great American Faunal Interchange. *Paleobiology* 17:266-280.
- Webb, D. S. 1997. The Great Faunal Interchange. In Central America: A Natural and Cultural History, ed. A. G. Coates, 97-122. New Haven, Yale University Press
- Yuan, D., et al. 2004. Timing, duration, and transitions of the last interglacial Asian monsoon. *Science* 304: 575-578.